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Electromagnetic Field of Microtubules: Effects on Transfer of Mass Particles and Electrons

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Abstract. Biological polar molecules and polymer structures with energy supply (such as microtubules in the cytoskeleton) can get excited and generate an endogenous electromagnetic field with strong electrical component in their vicinity. The endogenous electrical fields through action on charges, on dipoles and multipoles, and through polarization (causing dielectrophoretic effect) exert forces and can drive charges and particles in the cell. The transport of mass particles and electrons is analyzed as a Wiener-Lévy process with inclusion of deterministic force (validity of the Bloch theorem is assumed for transport of electrons in molecular chains too). We compare transport driven by deterministic forces (together with an inseparable thermal component) with that driven thermally and evaluate the probability to reach the target. Deterministic forces can transport particles and electrons with higher probability than forces of thermal origin only. The effect of deterministic forces on directed transport is dominant.

Key words: directed transport, electromagnetic fields in cells, organization in biology

Introduction

Organization of living matter is still not adequately understood. The many thousands of different chemical reactions carried out simultaneously and successively in living cells are closely coordinated. Reactions in the same as well as in different cellular compartments are linked together in chains and networks depending on the time and space coordinates. Electron transport is closely connected with biological activity. Electrons can be carried by diffusible molecules picking up electrons at one location and delivering them to another one as well as transferred along the molecular chains. The former mechanism is exploited in the mitochondrion and in the chloroplast using e.g. ubiquinone or plastoquinone as electron carriers. Transport of high-energy electrons inside the protein-pigment complex referred to as the photochemical reaction center is of the latter type. Mass and charge transports have fundamental significance for the function and activity of biological systems.

Mechanisms of motion and of transport of mass may be roughly divided into short range and long range ones. The short range mechanism acting e.g. between

reaction components in the reaction region contains recognition of reaction entities, of their active sites, the approach to a close distance, rotation and some kind of oscillatory motion, and preparation of linkages with respect to each other. London dispersion forces (interaction due to mutual polarization of the two components with respect to each other), thermal vibrations, rotations, and Brownian motion were assumed to be responsible for the short range arrangements in the reaction region. These factors may be highly specific and very strong in the vicinity of the source. Generally, random thermal motion was accepted as a general characteristic of these mechanisms. Deterministic reaction dynamics was not taken into consideration. Experimental data give evidence of coherent behavior. Coherent emission from myoglobin crystal was detected and described in [1], coherent vibrational motion was measured in some macromolecules (e.g. in deoxymyoglobin [2], and in bacterial cytochrome c oxydase [3, 4]). Coherent reaction dynamics described in [3] was measured at 442 nm for reactions of unliganded and CO liganded enzyme (bacterial cytochrome c oxidase). The transient absorption signal as a function of time exhibits coherent vibrational motion (at 47 cm^{-1}) which is related to haem a3 dynamics after photodissociation. The coherent motion is assigned to stepwise population of the product state. The reaction in a protein complex is driven by coherent motion. These facts suggest important function of vibrational coherence on the femtosecond and picosecond time scale. Excitation of quantum beats and generation of coherent infrared electromagnetic waves in the 10 THz band are described in [5].

Proteins have special properties based on their nuclear dynamics. Nuclear motion influences protein conformation resulting in different biological functions. Excitation by energy supply alters nuclear dynamics. Vos and his colleagues conclude that, on the time scale up to 1 ps, coherent vibrational motion conserving the phase for several periods of oscillations may be a general property of proteins and their fundamental functional feature [6].

Long range transport aimed at a certain target can have a considerable impact on the increase of probability of encounter and contribute to the organization of chemical reactions. Transport of organelles, vesicles, and other types of cargo by motor proteins (i.e., by kinesins and dyneins) along microtubules is directed at certain regions (the information system governing the transport is still not known). The transport along microtubules has a high degree of certainty over a long distance (i.e., over the scale range of the cell) but its rate is not high. Deterministic (coherent) endogenous forces could provide fast transport (within time scales less than a microsecond [7]) but the distance of transport is very likely shorter than that of motor proteins. The origin, nature, and properties of deterministic forces participating in the creation of order are still unclear.

Before we discuss charge transfer along molecular chains, we will discuss the electronic structure of DNA (deoxyribonucleic acid) and of proteins from a solid state physics point of view. Energies of the electron states in a molecule or in a solid as well as in a biological molecule or in a structure are split in many levels

and may form energy bands. The regular energy band structure is formed in a material with a strictly periodic lattice. Transfer of electrons from the valence (the highest filled energy band) to the conduction (the lowest unfilled) band depends on energy supply, e.g. by thermal excitation. The width of the gap between the valence and the conduction band (referred to as the forbidden band) determines the number of electrons in the conduction band. If we neglect the effects of donors, acceptors, traps, and radiation and if the width of the forbidden band is about 1 eV, the number of transferred electrons is limited and the structure has properties of an intrinsic semiconductor. The biological structures have quasi-periodic or correlated potential profiles (long-range correlation in DNA is discussed e.g. in [8–15]). Electron behavior may resemble that of conductivity electrons in semiconductors but with conduction band split in sub-bands and discrete levels. Transmission coefficient of electrons in DNA chains as a function of energy is e.g. in [16]. Donor-acceptor tunnelling and hopping mechanism in electron transport is assumed to exist in periodic nucleotide base stacks [17]. A polypeptide chain forms a protein backbone whose properties depend on the primary structure – on the amino acid sequence [18]. Delocalized electrons can move along the polypeptide chain or at least along part of it and mediate charge transfer in the structure. The sites of C_α atoms represent disturbances of periodicity due to different amino acid residua. The different conformations of the polypeptide chain play important role too. The β sheet is a two-dimensional system, and the resulting band structure is different from superposition of one-dimensional band structures. Ladik and Förner assessed band structures of some nucleotides and polypeptide networks [19]. The simple polypeptide chain of polyglicine has conduction and valence band widths of 1.38 and 2.1 eV [19], respectively. In the system with disturbed periodicity, the energy band structure is gradually disturbed, and eventually destroyed, with increasing disorder [19]. Analysis of some quasi-periodic structures shows high fragmentation of the transport coefficient (e.g. in Fibonacci superlattice [15]). In contrast, Bloch-like electronic states may be found in non-periodic structures (e.g. [20]) too.

Besides Brownian motion and activity of the motor proteins, intracellular oscillating electric field can drive transfer of molecules and particles [7]. Brownian type motion and electric potential difference can be driving agents for electron transfer inside molecules and structures as well. Frauenfelder *et al*. [21] analyzed forces in biological systems and claimed that "in biological physics, the force is known, it is electromagnetic interaction." Any molecule and any structure with electric dipole moment (and/or multipole moment) can generate an oscillating electric field with a dominant electrical component in its vicinity. It is well known that the majority of proteins are electrically polar and represent electric dipoles and/or multipoles. The strong electrically polar character of biological constituents makes possible longitudinal oscillations generating an electric field as was postulated by Fröhlich [22–24]. Energy supply from metabolic sources can excite vibrations far from thermodynamic equilibrium. Excitation depends on the amount of energy supplied to

the system, but not on the manner of its supply [25]. Analysis of the feedback loops in Fröhlich's system can determine excitation as a function of the intensity of pumping which need not be a linear function [26, 27]. Electron charge on delocalized orbitals may be important for the Fröhlich's mechanism. Generation of an endogenous oscillating electric field is analyzed in [28–31].

The hypothesis that electromagnetic forces have a fundamental role in the mechanisms of organization and transport of entities is supported by indirect and direct measurements of the electromagnetic fields around living cells. Pohl [32] observed attraction of small dielectric particles to cells and explained the results by dielectrophoretic effects. Rowlands *et al.* [33] found interaction forces between red blood cells up to a distance of about 1μm. Albrecht-Buehler [34] described the ability of cells to detect electromagnetic signals of other cells in the red or near-infrared range. Clusters of synchronized yeast cells in the M-phase sealed together by an electric field were measured by Del Giudice *et al.* [35]. Hölzel and Lamprecht [36] measured yeast cells in the frequency range of about 1–100 MHz. Measurement of the cellular electromagnetic field in the MHz range using special microelectronic sensors is described in [37]. The peaks of electromagnetic activity coincide with the development of the microtubule structure (mitotic spindle) in the M phase. Coherent vibrations of cellular membrane of yeast cells (*Saccharomyces cerevisiae*) were measured by atomic force microscopy at the frequency of about 1 kHz by Pelling *et al.* [38]. Vibrations are conditioned by metabolic energy sources of yeast cells.

A protein polymer network – the cytoskeleton – is a dynamic organizer of eucaryotic cells. The cytoskeleton exerts forces and generates movements without any major chemical changes. The cytoskeleton reorganizes continually as the cell changes its shape, divides, and responds to its environment. But the cytoskeleton might undergo dynamic changes by its internal development too. The fundamental structure of the cytoskeleton formed by microtubules satisfies the basic requirements for excitation of vibrations and generation of an endogenous oscillating electromagnetic field [28–31]. The oscillating electric field of microtubules could manifest itself by increased nonthermal forces around them in the cytosol that may affect the rheological measurements. Microrheological measurements using embedded tracer particle motion show that microscopic force generators may play a central role in the cell mechanics [39]. Forces may be generated by motor proteins. Probes (1–3 μm diameter microspheres) are driven by the collective activity of motor proteins [40]. The microtubule electromagnetic field should have a global character in the cell. The idea that large-scale forces are generated in yeast cells through the action of many proteins working in a concerted and cooperative manner is given in [38] too. The static electric field can be screened by ions in the cytoplasm. The oscillating electric field cannot be effectively screened if the activity of the ions is low with respect to the frequency of oscillations.

In this contribution we will overview the fundamental data of the microtubular structure in the eucaryotic cell from the point of view of generation of the

endogenous electromagnetic field, and present theoretical analysis of directed transport of mass and charge by the field.

Microtubules as Generators of an Oscillating Electrical Field

Fröhlich postulated long-range quantum mechanical phase correlations in biological systems and excited longitudinal oscillations as stabilising modes. Fröhlich's theory is based on three foundation stones: extraordinary polar properties of biological structures, spectral energy transfer between vibration modes with participation of the heat bath (conditioned by non-linearity of the system), and energy transfer to the system (energy supplied is not entirely thermalized and may condense in certain vibration modes) [22–24]. Microtubules in living cells seem to comply with Fröhlich's postulate. A schematic picture of a part of a microtubule is shown in Figure 1a. Each heterodiomer subunit of a microtubule (tubulin heterodimer) binds 18 calcium ions [41–43] and its dipole moment is greater than 1000 Debye (10^{-26} Cm). The induced dipole moment per dimer arising only from the motion of mobile electrons or protons was estimated to be 200–400 Debye [44]. The orientation of the dipole moment is changed after hydrolysis of GTP (guanosine triphosphate) to GDP (guanosine diphosphate) in the β-tubulin (Figure 1b). Vibrations in the structure generate an oscillating electric field around it. Energy is supplied to the microtubule structure by hydrolysis of GTP to GDP in β tubulins [45, 46]

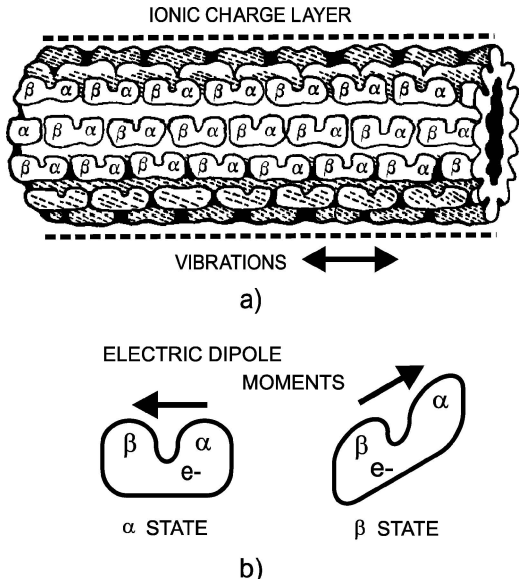

Figure 1. A schematic picture of a microtubule formed by protofilaments composed of tubulin heterodimers (a). Heterodimer in the α and the β conformation state; the arrows denote the vectors of the electrical dipoles (b). After [31].

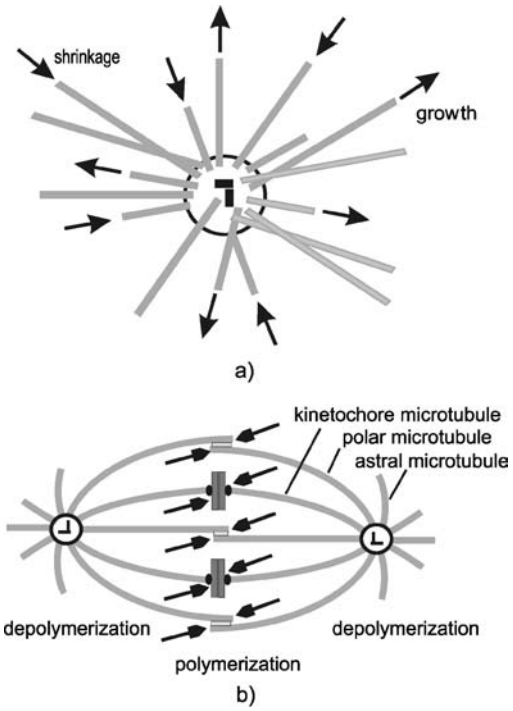

Figure 2. The microtubular structure in the interphase (a) and in the M phase (b). In the interphase (a) microtubules display dynamic instability (the growth and the shrinkage of their body indicated by arrows). In the M phase treadmilling causes polymerization from one side (from the center indicated by arrows) and depolymerization from the other side (at the poles of the mitotic spindle). Both processes exchange heterodimers with exhausted energy for energy-rich ones and provide energy supply to the structure. After [31].

and, therefore, vibrations could be excited [29, 30]. Heterodimers with exhausted energy are replaced by energy-rich ones by the mechanisms of dynamic instability and of treadmilling (Figure 2). From the energy released by hydrolysis, 7.1 kJ mol^{-1} [45, 46] is stored in the microtubule. Taking into account the average growth rate of the microtubule (i.e. rate of exchange of microtubule subunits) in the interphase, the energy supplied within 1 s (i.e. power) may be 10^{-14} Wcm $^{-1}$ [30, 31]. In the M phase of the cell cycle the rate of energy exchange of heterodimers is more than one order of magnitude greater than that in the interphase, and this increase of rate corresponds to the increase of energy supply. Activity of motor proteins could supply energy to the microtubular structure as well.

Viscosity damping of vibrations in microtubules is minimized by the slip layer at the boundary between the microtubule and cytosol. The slip layer is conditioned by large deformability of microtubules at low stress and by attraction of ions to their surface and formation of an ionic layer [30, 31].

Mass and Charge Transport

Transport of mass and charges in biological systems may be driven by random forces of the thermal motion and by deterministic forces exerted by the electrical field (which acts on charges, electrical dipoles and multipoles, and through dielectrophoretic effect on neutral mass particles). We assume that the deterministic motion and the random thermal motion may be treated independently. In this description we separate the random force of thermal motion from the deterministic force (causing directed transport) and the resulting motion can be characterized as a Wiener-Lévy process which is a limit form of the random walk [47] (nevertheless, directed transport in a randomly organized chain may also exist due to breaking the symmetry of the Wiener-Lévy process [7, 48]). We will use a one-dimensional approximation. The probability density $f(x;t)$ of the Wiener-Lévy process is given by the relation

$$f(x,t) = \frac{1}{\sqrt{2\pi\alpha t}} \exp\left(-\frac{(x-vt)^2}{2\alpha t}\right) \tag{1}$$

where t is time, x is distance, and αt the variance. For the transport of spherical mass particles (with radius sufficiently large) the velocity v and the variance parameter α may be determined from Stokes' law in the form

$$v = \frac{F}{6\pi\eta r}, \quad \alpha = \frac{k_B T}{3\pi\eta r}$$

where F is the deterministic force, η is the dynamic viscosity, r is the radius of the particle, T is the temperature, and k_B is the Boltzmann constant. (Significance of directed transport of mass particles to the target region under action of deterministic forces is discussed in [7].)

We will determine v and α for electron transport in molecular chains too. Besides the assumption that the Wiener-Lévy process describes diffusion with deterministic motion we assume that the Bloch theorem may be used. Therefore, we will use the solid state theory of periodic structures as is described e.g. in [49]. The variance parameter is given by $\alpha = s^2/\Delta t$, where s is the length and Δt is the time interval of the elementary step. In our case s is the mean free path of electrons and $\alpha = sv = sh^{-}|\boldsymbol{k}|/m^*$, where m^* is the effective mass, and $|\boldsymbol{k}| = k = 2\pi g/(aG)$ is the absolute value of the reduced wave vector (a is period of the lattice, G the number of particles in the lattice, and g is an integer). The probability density of finding electron at x is given by the sum

$$f_e(x;t) = \frac{R}{A}\sum_k \frac{1}{\sqrt{2\pi\alpha(k)t}} \exp\left(-\frac{\hbar^2|\boldsymbol{k}|^2}{2m^* k_B T}\right) \exp\left[-\frac{(x-v(k)t)^2}{2\alpha(k)t}\right] \tag{2}$$

where the normalization factor $A = \sum_k \exp[-(\hbar^2|\boldsymbol{k}|^2)/(2m^* k_B T)]$ and R stands for the change of probability caused by trapping and recombination processes which may be represented by the factor $R = \exp(-t/\beta)$ (β is the relaxation time). In Eq. (2) and in the relation for A the Fermi-Dirac distribution is approximated by the Botzmann one. Velocity $v(k)$ in (2) is given by relation $v(k) = \mu(k)E$, where E is the intensity of the electrical field, and the electron mobility μ may be determined from the relation

$$\mu = \frac{se}{2k_B T A} \sum_k \frac{\hbar|\boldsymbol{k}|}{m^*} \exp\left(-\frac{\hbar^2|\boldsymbol{k}|^2}{2m^* k_B T}\right) \tag{3}$$

where e is the elementary charge. The Einstein relation for the diffusion coefficient was used to derive Eq. (3).

Results

We evaluated the probability $f(x;t)$ and the probability P for transport of spherical particles (molecules) driven by the force of thermal motion and by deterministic force. Figure 3 shows probability density $f(x;t)$ of finding a particle with radius r at a distance x. Time t is a parameter. The density $f(x;t)$ is spreading with increasing time. The dotted line denotes a path with length of 15 nm. No deterministic force is assumed ($F = 0$). The effect of a deterministic force is shown in Figure 4a ($F =$ 1 pN, i.e., intensity of the electric field 10^7 Vm^{-1} acts on the elementary charge by a force of about 1 pN) and Figure 4b ($F = 10$ pN). The deterministic force is directed from the point 0 to 15 nm and the probability density curve is shifted in the direction of action of the force. The target is assumed to be positioned at the distance 15 nm

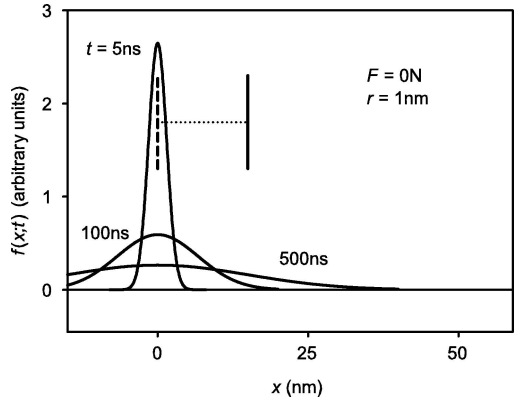

Figure 3. Probability density $f(x;t)$ as a function of distance x. Time t is a parameter. The probability density spreads as a result of thermal motion. No deterministic force is applied. Radius r of the mass particle is 1 nm.

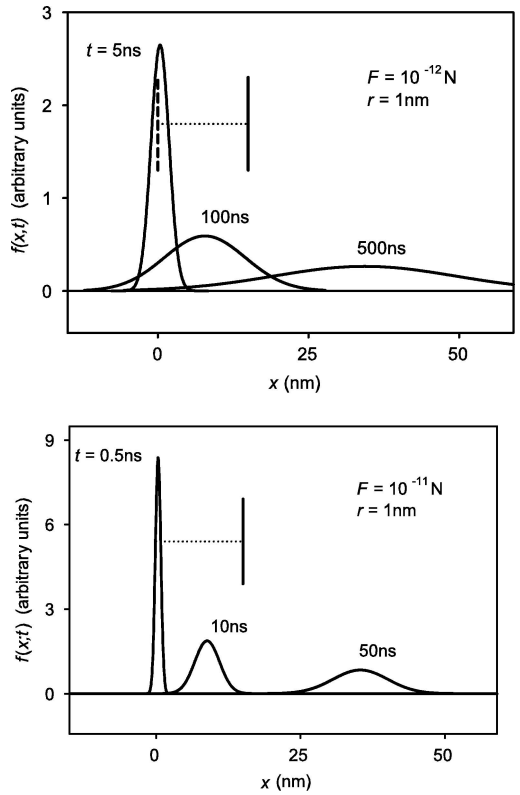

Figure 4. Probability density $f(x,t)$ as a function of x shifted by a deterministic force F. Time t is a parameter. Radius r of the mass particle is 1 nm. a) $F = 1$ pN, b) $F = 10$ pN.

and the curve $f(x;t)$ moves to the target. The greater the force F the shorter the time interval to reach the target and the smaller spreading of the $f(x;t)$ curve (Figure 4b). The integral of the part of the probability density curve behind the full line at 15 nm denotes the probability that the particle reaches the target. Figures 5a and b show probability (P as a function of time t) that the particle can reach the target. The probability of a particle driven by a deterministic force to reach the target is greater than in the case with no deterministic force. The greater the force, the greater the shift of the probability density curve, and the greater the probability. For the deterministic force 10 pN (Figure 5b) a particle of a diameter 2 nm is transported over a distance about 50 nm within a time interval of about 0.1 μs with probability $P \approx 1$ (which is nearly a certain event). Motion driven by deterministic force increases probability to reach the target region in comparison with random thermal motion.

Figures 6a and b show probability P as function of time t that an electron will reach the target region at a distance d. The distance d is a parameter. The mean free path of the electron is $s = 1$ nm. Intensity of the electrical field is 10^6 (Figure 6a) and 10^7 Vm^{-1} (Figure 6b). For the electrical field 10^6 Vm^{-1} considerable effect

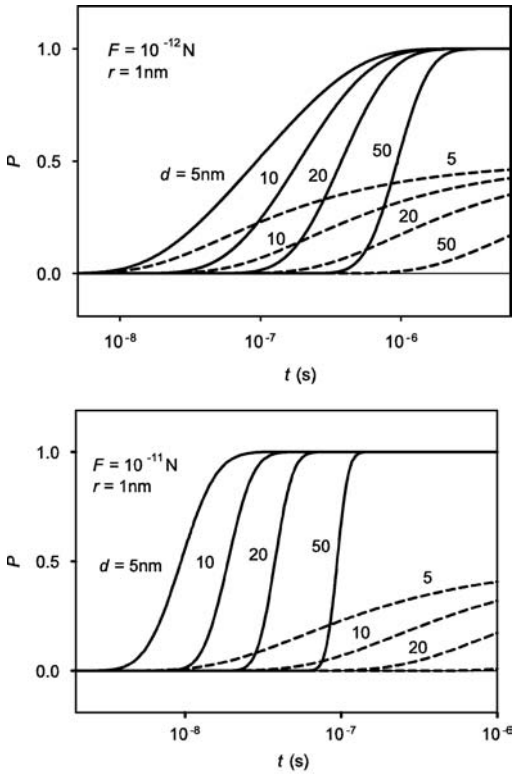

Figure 5. Probability P that a mass particle will reach the target region as a function of time t. The length d of the path is a parameter. Radius r of the mass particle is 1 nm. The dashed and the full curves denote motion driven by thermal forces and motion driven by thermal and deterministic forces, respectively. a) $F = 1$ pN, b) $F = 10$ pN.

of thermal motion is visible. Electrons may be shifted over a distance about 20 nm by the electrical field within a time interval less than 10 ps with probability near to 1 (Figure 6b).

Discussion

Wiener-Lévy theory was used to assess the effect of deterministic forces on the directed transport of mass and charge in comparison with the effects of thermal forces. A one-dimensional approximation was used. A more general assessment may be obtained from Kolmogoroff diffusion equations [47]. Nevertheless, even one-dimensional analysis presented in this contribution shows that deterministic processes of electrical nature might play a dominant role in organization in biology. Mass transport of small particles is presented in this contribution. We analyzed transport of bigger particles as well. As a particle's velocity decreases (proportional to r^{-1}) the time for high probability transport is longer, but adequately more

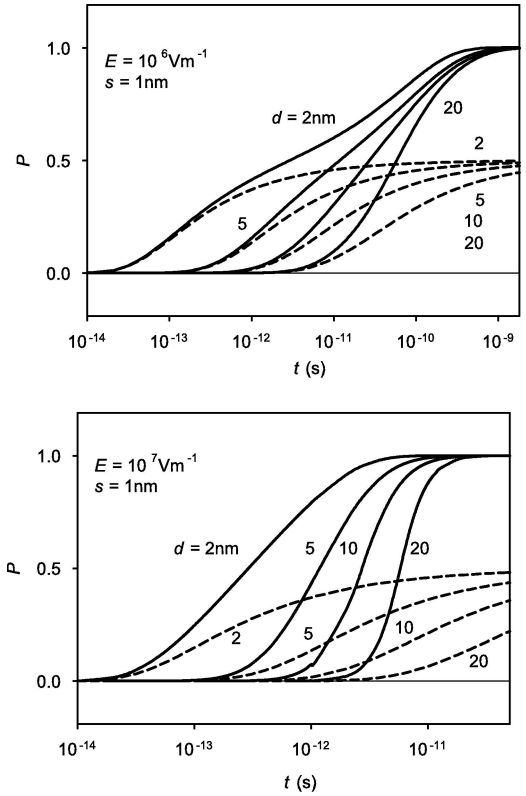

Figure 6. Probability P that an electron will reach the target region as a function of time t. The dashed and the full curves denote motion of an electron driven by thermal forces, and by thermal forces and the electrical field E, respectively. a) $E = 10^6$ Vm^{-1}, b) $E = 10^7$Vm^{-1}. Electron driven by electrical field can reach the target at a distance 20 nm within a time interval less than 10 ps with the probability about $P \approx 1$ (Figure 6b).

effective in comparison with the thermal one. Transport of electrons is analyzed with the assumption of perfect translation symmetry without inclusion of the surface states. Validity of the results might be limited to shorter regions of the molecular chains. But in short chains the surface states might have prevailing effect. Symmetry disturbances can cause large alterations of the band structure and of the transport as well. Recombination of electrons may have significant effect if the time period of transport is comparable with their life-time. As far as the life-time is about 1 ns the transport on the scale of 0.1 ns or shorter cannot be significantly disturbed. The large magnitude of the deterministic force is important for high probability of the directed transport. The smaller the deterministic force, the smaller the probability, and the greater the disorder. The decrease of probability of directed transport might explain some pathological states displaying large disorder.

We analyzed transport of electrons in the molecular chains outside the regions of redox potential taking into account forces of random thermal motion and

deterministic forces. The redox potential (a measure of the electron carrier's affinity for electrons) is important in the donor and acceptor events representing the start and the end of the transport, respectively. Outside the redox potential region, the random and deterministic mechanisms of transport are important. Energy of the thermal noise is many orders of magnitude greater than energy of the deterministic motion but due to random character the final effect is isotropic (not oriented to the target) and the probability of long range directed transport is small. Nevertheless, thermal noise can help to overcome potential barriers. Deterministic motion driven by the electrical field regardless of the small energy, in comparison with that of thermal noise, mediates directed transport to the target with high probability to reach it.

Conclusions

Electrical polar structures inside the cell with energy supply (such as microtubules) can become excited and generate an endogenous electric field. Endogenous electric field can have dominant effect, on directed transport of molecules and electrons such that the probability to reach the target is enhanced in comparison with random thermal motion.

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